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THE REAPPEARANCE IN THE OFFSPRING OF ARTIFICIALLY PRODUCED PARENTAL MODIFICATIONS [1]

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IN a recent paper[2] I have described a series of experiments conducted during the past few years upon white mice. I have there shown that large enough differences of temperature, operating throughout the period of growth, bring about considerable, and in some cases quite obvious, differences in the length of peripheral parts (tail, foot and ear), and probably changes in the quantity of hair as well. The peripheral parts were found to be longer in the warm-room lots (12 to more than 30 per cent. longer, in the case of the tail); the amount of hair, on the contrary, was less. It was pointed out, furthermore, that differences of precisely this sort have long been known to distinguish northern from southern races of mammals.

The question of most vital interest was not, however, touched upon in the earlier paper, although it has furnished my real motive for pursuing these experiments throughout. Are these modifications purely transitory,

[1] This rather cumbersome title has been chosen in order to forestall any possible misrepresentation of my claims by those who do not read beyond headlines. Note that I have used the word "*reappearance*," rather than "*inheritance*."

[2] *Journal of Experimental Zoology*, August, 1909.

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that is to say confined to the generation immediately affected, or do they reappear, if only to a slight degree, in the offspring? I have long felt that satisfactory evidence for or against the transmission of such modifications would be lacking, so long as zoologists confined themselves to a search for directly visible *qualitative* differences. With few exceptions, however, such has been the method by which the problem has been attacked.

The following conditions must, I believe, be realized before we may hope to attain to any satisfactory test of this time-honored question: (1) We must select for experiment such an organism and such a physical agency that the latter may modify the former without directly influencing the germ cells. The action of temperature upon a warm-blooded animal seems to realize this condition most fully. (2) We must discover readily measurable, *quantitative* changes in the parent generation, before we can hope to test the reappearance of such changes in the offspring.

Having discovered such modifications in the parent generation, there are theoretically two methods by which we may attack the problem in hand. We may either (1) raise the offspring of the experimental and control[3] lots under identical conditions, or (2) we may raise the offspring of the modified parents under the same conditions as were employed to effect the original modification. In the first case, we should compare the two sets of animals having different parentage. Assuming a given modification of the value x, and supposing that $1/n$ represented the proportional part of this to be transmitted, the offspring of the two lots would be found to differ by the quantity x/n. If the second method were employed, we should compare the second generation with the parent generation, the two being measured at the same age.

[3] For the sake of simplicity I have here assumed that one lot was merely a "control" lot, *i. e.*, exposed to normal or indifferent conditions. In my own experiments, however, I have chosen conditions with a view to modifying both sets of individuals in opposite directions.

Assuming that the latter had been modified to the extent x, the former, according to hypothesis, would be found to be modified to the extent $x + x/n$; *i. e.*, the effect of the conditions would have been cumulative.

Now, as a matter of fact, I have attempted both of these tests upon rather a large scale; but I have not yet found the second one to be practicable, owing to the difficulty, without special facilities, of repeating precisely the same temperature conditions during the lives of two successive generations. But the first test proved to be practicable, and has yielded the results which are summarized in the ensuing paper. Since the full data are to be published elsewhere in the course of the coming year, the omission of certain important portions of the evidence will, I trust, be condoned.

The parents of the mice to be discussed had been divided, at the commencement of life, into two lots, which were reared in separate rooms, differing widely in temperature.[4] Prior to the time of the pairing, they had been exposed to these conditions for an average period of about six months. For reasons which I shall not here state, the two contrasted groups ("warm" and "cold" lots) were not transferred to a common room before pairing.[5] Indeed, the females were not removed to such a room until the time that each was discovered to be pregnant. The discovery was made, on the average, about five days before the birth of the young, *i. e.*, about two weeks after the actual commencement of pregnancy. This circumstance is of possible importance in interpreting the results obtained. On that subject, more anon.

From the time that pregnancy became apparent, the mothers of the two lots were kept in the same room and under conditions which were identical, so far as care could make them so. Differences of temperature were particularly guarded against.

[4] Differing by at least 15° C., on the average. The exact figures are not yet computed.

[5] The differences in temperature between the two experimental rooms were, however, very much reduced at this time.

The young were measured at the age of forty-two days. It was found to be impracticable to make certain of these measurements satisfactorily without subjecting the animals to ether. They were not, however, killed at this time. The weight, and the length of tail, foot and ear were determined. The linear measurements were taken with a graduated sliding caliper, indicating tenths of a millimeter. In the case of foot and ear, two measurements were made of each, the mean figure being employed in the computations.[6]

Of these mice, 286 survived to the age of six weeks; there being 141 offspring of warm-room parents, belonging to 33 litters, and 145 offspring of cold-room parents, belonging to 30 litters. From this earlier series of measurements the following gross averages were obtained:

	Weight (grams)	Tail (mm.)	Foot (mm.)	Ear (mm.)
Cold-room descendants	10.897	71.04	17.833	12.434
Warm-room descendants	10.631	71.19	17.960	12.536

It will be seen at once that, although the offspring of the warm-room mice average slightly less in weight, they have slightly longer tails, feet and ears than the offspring of the cold-room mice. These differences are exactly such as were noted, on a larger scale, in the parent generation. But such gross averages do not, in themselves, mean very much. In each of the contrasted groups are comprised individuals of widely different size (the extremes were 6.5 and 19.3 grams). Our material, therefore, is not at all homogeneous.

Accordingly, I have divided the animals into groups, comprising individuals of approximately the same weight.[7] Herewith are presented in tabular form the results of such an analysis.

From the table it will be seen that there are eleven groups in which a comparison between warm-room and

[6] The average difference between the first and second reading of the caliper was 0.19 mm. for the foot, and 0.12 mm. for the ear.

[7] In my complete table I have likewise dealt with the sexes separately. Lack of space prevents this procedure here.

cold-room descendants is possible. The mean tail length for the former animals is greater in eight of these eleven cases (exceptions starred); the mean foot-length is greater in nine of the eleven cases; while the mean ear length is greater in nine cases, and equal in one case. Let us consider the likelihood that such results have been obtained through "chance." What are the probabilities that, in tossing a coin, we shall throw "heads" or "tails" as many as eight times out of eleven? The chances that we shall obtain as great an excess as this (on one

Group.	Parentage.	Number of individuals.	Weight.	Tail.	Foot.	Ear.
6–6.9 gms.	Cold	2	6.55	59.00	16.950	11.900
	Warm	3	6.77	60.67	16.800*	11.850*
7–7.9 gms.	Cold	12	7.57	61.91 ±0.79	16.954 ±0.110	11.850 ±0.076
	Warm	16	7.58	65.37 ±0.51	17.319 ±0.082	12.037 ±0.047
8–8.9 gms.	Cold	9	8.51	64.78 ±1.23	17.356 ±0.110	12.217 ±0.054
	Warm	19	8.48	67.11 ±0.45	17.642 ±0.052	12.313 ±0.054
9–9.9 gms.	Cold	23	9.41	68.65 ±0.57	17.572 ±0.069	12.311 ±0.035
	Warm	18	9.51	71.29 ±0.30	17.906 ±0.041	12.533 ±0.034
10–10.9 gms.	Cold	32	10.51	71.47 ±0.39	17.962 ±0.069	12.491 ±0.037
	Warm	27	10.33	70.41*±0.47	17.931*±0.050	12.559 ±0.043
11–11.9 gms.	Cold	27	11.42	73.62 ±0.36	17.975 ±0.063	12.534 ±0.0 5
	Warm	17	11.38	73.06*±0.38	17.994 ±0.057	12.568 ±0.085
12–12.9 gms.	Cold	16	12.46	73.37 ±0.66	17.844 ±0.100	12.544 ±0.065
	Warm	18	12.39	73.67 ±0.42	18.122 ±0.052	12.783 ±0.053
13–13.9 gms.	Cold	14	13.31	74.54 ±0.79	18.200 ±0.094	12.629 ±0.069
	Warm	12	13.32	76.33 ±0.46	18.504 ±0.052	12.842 ±0.083
14–14.9 gms.	Cold	3	14.30	75.67	18.333	12.617
	Warm	2	14.20	77.00	18.725	12.700
15–15.9 gms.	Cold	2	15.25	79.00	18.825	12.750
	Warm	6	15.40	77.33*	19.000	13.067
16–16.9 gms.	Cold	3	16.20	79.33	19.100	13.050
	Warm	3	16.37	83.00	19.217	13.050*
19–19.9 gms.	Cold	1	19.30	89.00	19.700	13.200
	Warm	0				

side or the other) are about 5 out of 22. This is admittedly not a very unlikely happening. The chances that nine of the eleven will be of one kind are about 1 in 15.

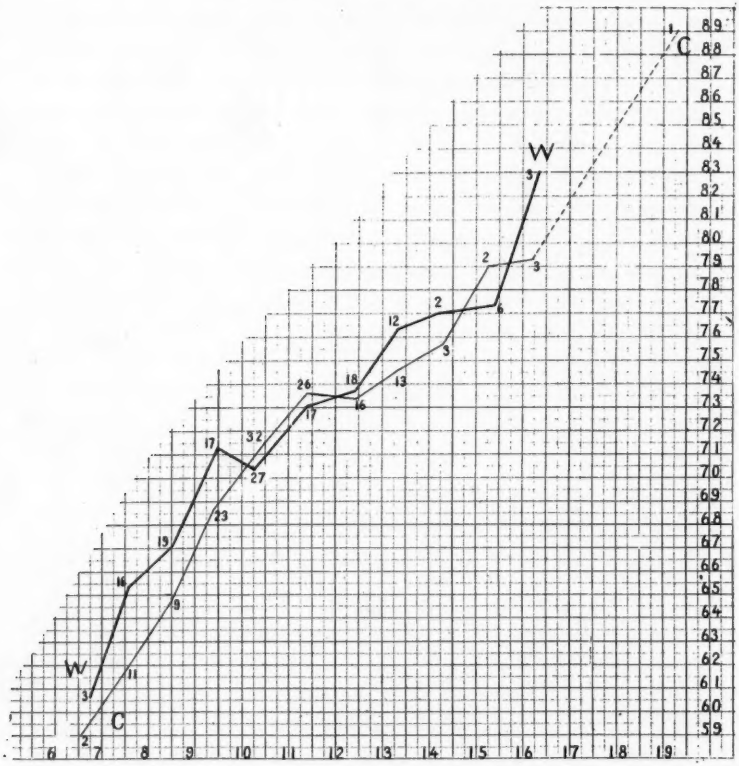

FIG. 1. Curves showing mean tail length in relation to the size of the animals. The heavier line (*W*) represents the condition in the offspring of warm-room parents, the lighter line (*C*) representing that in the offspring of cold-room parents. Abscissas denote weight in grams; ordinates denote tail length in millimeters. The figures along the curves denote the number of individuals in each size-group.

Finally, the chances that we shall obtain as high a proportion as nine out of ten[8] of the same sort are only 2 in 93.

It must be borne in mind, however, that we have the cumulative testimony of these three characters, all point-

[8] The group in which the two contrasted lots showed an *equal* ear-length has been left out of account. This would correspond to the case of a coin remaining poised *edgewise*. In our probability estimates we have not contemplated such a contingency.

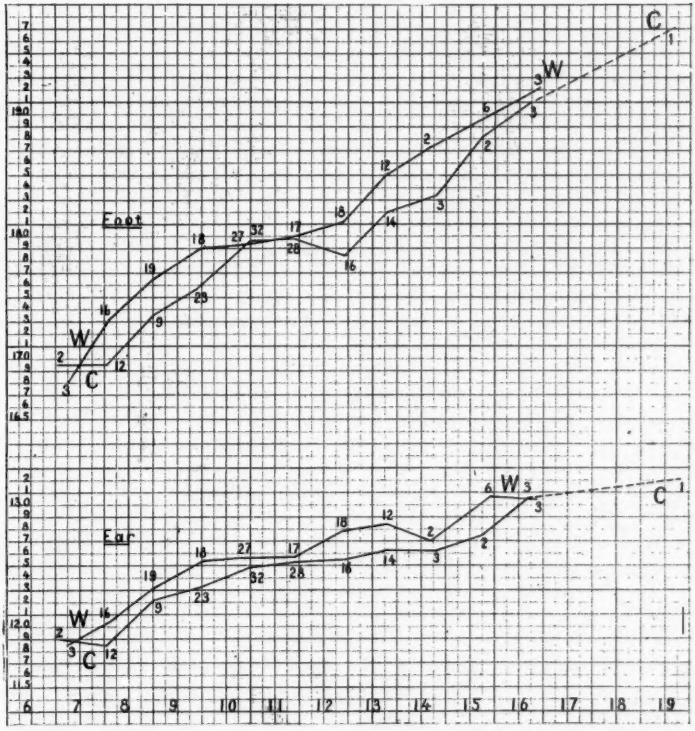

FIG. 2. Curves showing mean foot and ear length. The upper line (*W*) in each case is that showing condition in offspring of warm-room parents. For further explanation see Fig. 1.

ing in the same direction; *i. e.*, we have 26 out of 33 cases showing the same tendency. If we assume that these parts vary quite independently of one another,[9] and if we leave out of consideration the single case of equality, the probability of our obtaining such a large majority in a purely "accidental" way is only 1 in 1,869. In most of the practical affairs of life, we should reject such a contingency as not worth considering.

[9] In reality, there is a certain degree of correlation between them, the extent of which has not been computed. This would render the chances somewhat greater than is here indicated.

Thus far, we have treated these groups as of equal value in our computations. From our table it will be seen, however, that the groups differ greatly in respect to the number of individuals comprised, and in respect to the magnitude of the differences shown. I have computed the probable errors of the averages for those seven groups which are large enough to make this worth while. Taking into account the three characters (tail, foot and ear) for the seven groups, we have, accordingly, twenty-one probable errors for each of the contrasted sets ("warm" and "cold"). A little figuring shows that in twelve of these twenty-one cases the difference between two contrasted averages is two or more times as great as the probable error of that difference; in one case the difference is over three times its probable error, and in three cases it is over four times its probable error.[10] The significance of these facts will be appreciated by any one familiar with statistical methods.

Diagrams (Fig. 1 and 2) have been constructed permitting of a comparison between the two contrasted sets of mice, with respect to the mean length of tail, foot and ear, for each of the size groups. These curves explain themselves, and further comment seems unnecessary.

The question naturally arises: How do these differences between the warm-room and the cold-room descendants compare in amount with the differences which were shown by the parents as a direct result of the external conditions? Unfortunately, the data necessary for a direct reply to this question are not at hand, since, in the case of the parents of this particular lot, foot and ear length were not determined at the age of six weeks. I have at hand, however, a set of measurements for a considerable number of mice (80 "cold" + 129 "warm"), which were subjected to substantially

[10] It is important to note that in none of the exceptional cases (*i. e.*, those in which the cold room descendants have *longer* peripheral parts) is the difference between the averages as high as two times its probable error. In one case it is practically equal; in another it is considerably less.

the same temperature conditions as were these parents. To determine the extent of the differences, we shall consider, not the differences between the gross averages, for reasons already stated, but the average difference, within each size group, between the "warm" and the "cold" figure. These mean differences, representing the extent of the modification shown at the age of six weeks by mice directly influenced by temperature are:

Tail	9.710	mm.
Foot	0.7138	mm.
Ear	0.2021	mm.

Corresponding figures for the warm-room and cold-room descendants with which we have been dealing are:

Tail	1.264	mm.
Foot	0.1890	mm.
Ear	0.1281	mm.

Comparing these two sets of figures, we find that the difference in tail length is 13 per cent. as great in the second case as in the first; the difference in foot length is 26 per cent. as great, while the difference in ear length is 63 per cent. as great! These figures are not offered as expressing, with even a rough degree of approximation, the proportional part of these parental modifications which is handed on to the offspring—even granting that such a transmission occurs. The relative magnitude of these three percentages is particularly surprising, in view of the fact that the tail is the organ which responds most decidedly to the temperature differences, while the ear has been shown to be least affected.[11] It might be argued that the very plasticity of a part, which makes it so responsive to outside influences, might render it correspondingly ill adapted to retaining such impressions permanently.[12] Such speculations are decidedly premature, however.

[11] In my earlier paper I even expressed doubt as to the significance of those slight differences which I did find in the case of the ear. Further observations have, however, lessened these doubts.

[12] It must be pointed out that the tail is far more variable than either the foot or the ear.

Another set of measurements was made with this same lot of mice when they reached the age of three months. By that time the numbers had been considerably reduced by death. There were at the later date 114 of the cold-room descendants, and only 84 of the warm-room descendants. The survivors all appeared to be in good health, however.

In order to exclude the possible influence of suggestion or unconscious bias in determining these rather delicate caliper measurements, I adopted the plan of keeping myself in ignorance as to the parentage of each mouse until the latter had been measured.[13]

I shall not at present enter into as full an account of these later measurements as of the first series. The differences between the gross averages are even less to be relied upon here than in the case of the earlier figures, since the two contrasted lots differed much more in their mean size. The warm-room descendants were somewhat the heavier of the two, having a mean weight of 19.45 grams, as compared with 18.56 grams for the other lot. The body length was also somewhat greater for the former (87.683 mm.) than for the latter (86.703 mm.). For statistical purposes, the animals have been grouped in two different ways: (1) according to weight, as was done previously, and (2) according to body length.[14] The latter method of grouping seems a much fairer one than the first, for it is probable that the length of the appendages is correlated primarily with body length, and only incidentally with weight. The single weight-groups, it may be added, contained individuals which differed from one another by as much as 4 or 5 mm. of body length.

To consider the second of these methods first, the animals were divided into groups, within each of which the

[13] The animals were put into separate small cages, each bearing an identification mark upon the bottom. These cages were "shuffled" by one or another of my colleagues in the laboratory.

[14] The mice were killed at the time of these later measurements. For this reason it was possible to determine the body length with accuracy. This is not feasible with living animals, even when etherized.

individuals differed by less than one millimeter in length. Of these groups there are 15 which allow of a comparison between cold-room and warm-room descendants. Now the "warm" figures for tail, foot and ear are larger than the "cold" figures in 12, 11 and 10 cases out of the 15, respectively. The chances for the "accidental" occurrence of such majorities (in either direction) are roughly 1 in 28, 2 in 17, and 3 in 10, respectively. The cumulative improbability, as regards the three cases, is very high, but the exact chances have not been computed.

The results to be derived from a consideration of the weight groups need not be detailed here. It must be stated, however, that the figures, although showing the same general tendency as those we have considered, are not, in themselves, as convincing as were the earlier ones. Indeed, when the size groups are broken up into subgroups according to sex, the figures, for the males, at least, are somewhat equivocal.

Thus, while the results of these latter measurements on the whole confirm the results obtained earlier in life, they are not as striking as those, and, if taken by themselves, could not be regarded as demonstrative. This is due, in part, to the fact that we are dealing with smaller numbers of individuals. It is probably also due, in part, to the principle of the "leveling down of initial differences," concerning which I have had much to say in my earlier paper. And lastly, it is possible that unconscious bias in the use of the calipers may have somewhat exaggerated the differences shown in the earlier series of measurements, although caution was taken to avoid this.[15]

Interpretation

Aside from delusion or deliberate prevarication on the part of the writer, several interpretations of these results seem theoretically possible.

[15] The caliper scale was at all times invisible to me until the points of the instrument were finally adjusted. Personally, I regard any such bias in making these measurements as improbable; but it can not be rejected as impossible.

1. The differences may be due merely to "coincidence" or "accident." The odds against such an occurrence have been shown to be high. Indeed the cumulative improbability that all of these differences have been accidental is enormous.

2. They might have resulted from a slight though constant biasing of the measurements in favor of that result which was calculated to give the greatest personal satisfaction. This possibility, which has already been considered, has been excluded in the case of the second series of measurements.

3. Granting their genuineness, the differences may be due, not to any specific influence (hereditary or otherwise) which has affected the tail, foot or ear directly, but to some general constitutional difference in the offspring of the two sets of parents. In other words, these differences in the length of the peripheral parts may be *correlated* with some constitutional difference of a very general sort. In this connection, it must be admitted that the offspring of the warm-room mice showed a very much higher mortality (40 per cent. between the first and second measurements) than those of the cold-room mice (20 per cent.). The former were likewise somewhat larger, on the average, when measured at the age of three months. Thus there did exist some sort of a constitutional difference. The possibility here considered can not, therefore, be set aside. On the other hand, there is absolutely no evidence in its favor.

4. An explanation closely similar to the last would be that the general stage of development in one lot of mice had been accelerated or retarded as compared with that of the other. We know that the ears and feet of young mice are relatively much larger than those of older ones. It might be contended, therefore, that the warm-room descendants were in a relatively more juvenile condition, despite the fact that they were, on the average, no smaller (*larger,* indeed, at the time of the later measurements).

Even this possibility can not be dismissed without a hearing.

5. The offspring themselves, during their fetal life, may have been influenced in some way by the differences of temperature to which the mothers were subjected during the first two weeks of pregnancy (see above). It is obvious, however, that in a warm-blooded animal, the fetus could not be directly affected by differences of temperature *as such*. It would be curious, indeed, if the parental modifications should be so closely paralleled under these circumstances.

6. The germ-cells of the parents may have been so affected by the external conditions to which the latter were subjected that modifications resulted in the offspring similar to those which were produced in the parents directly. This hypothesis has been invoked again and again to account for a certain class of facts which would seem at first sight to lend strong support to the Lamarckian hypothesis, *e. g.*, by Weismann and by Tower. Such an explanation could not, however, be applied in the present case without radical modification. For we may again point out that in a warm-blooded animal differences of temperature, *as such*, could not affect either the fetus or the germ-cells to any appreciable extent.[16] The suggestion might be made, however, that the effects of temperature, even upon the parent body itself, may not be direct, but may be due to the formation of specific chemical substances which, through the medium of the blood, may be supposed to simultaneously influence the body and the germ-cells. Such a hypothesis can neither be proved nor disproved in the present state of our knowledge, but it is perhaps the type of explanation which is calculated to appeal most strongly to the biologist of to-day. It may be pointed out, however, that *if a mech-*

[16] Pembrey (*Journal of Physiology*, Vol. XVIII, 1895, pp. 363–379) found the temperature of adult mice to remain constant at widely different external temperatures. In the young, however (under ten days old), the body temperature was found to vary with that of the atmosphere.

anism exists whereby the germ-cells may be so influenced as to bring about the parallel modification of parent and offspring, such a mechanism would be of exactly the same value for evolution as the "inheritance of acquired characters" in the old sense. For heredity, however, the case would be different. We should still be able to go on talking about the "continuity of the germ-plasm," though that expression would have been shorn of much of its meaning.

7. Finally, we have the view that the changes undergone by the parent body are in some way registered in the germ-cells, so as to be repeated, in a certain measure, in the body of the offspring. The "classical" attempt to make this process intelligible is of course Darwin's hypothesis of "pangenesis." Other views have been put forward recently[17] which are scarcely to be distinguished from the preceding type of explanation (no. 6).

It would not be profitable to enter into any scholastic discussion of these various hypotheses. One after another of these alternatives must be excluded by carefully planned experiments; and it is the intention of the present writer to continue such experiments on a much greater scale in the near future.

November 6, 1909.

[17] *E. g.*, by Cunningham, Archiv für Entwicklungsmechanik, 1908.

A BIMODAL VARIATION POLYGON IN SYNDESMON THALICTROIDES AND ITS MORPHOLOGIL SIGNIFICANCE

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IN the spring of 1906 I had occasion to count the number of leaf laminæ in the involucres of a series of four hundred inflorescences of *Syndesmon thalictroides* collected from the north slope of a hill at Meramec Highlands, Missouri. In making the records, each distinct lamina was counted, whether it was leaf or leaflet, the immediate purpose of the work being to get some idea of the variability in the number of divisions of the leaf surface in the involucral whorl and the degree of interdependence of the number of laminæ and the number of flowers for comparison with studies already made of the correlation between length of stalk and number of flowers per umbel in Nothoscordium and Allium,[1] and between number of flowers per inflorescence and number of ovules or seeds per ovary in Cercis[2] and Celastrus.[3] When I gathered the material I was quite aware that this rough method of lumping the laminæ is not suited to bring out the morphological significance of the data, but only a little time was available for the work and for the purpose then in hand the method of treatment seemed quite adequate.

These data are shown in the form of a correlation surface in Table I.

It is quite unnecessary to publish graphs for these two distributions to show the conspicuously bimodal character. For the number of laminæ, there are conspicuous

[1] Harris, J. Arthur, *Ann. Rept. Mo. Bot. Gard.*, Vol. XX, 1909.

[2] Harris, J. Arthur, *Biometrika.* In press.

[3] Harris, J. Arthur, *Ann. Rept. Mo. Bot. Gard.*, Vol. XX, 1909.

modes on 4 and 6, and for the number of flowers, pronounced modes on 1 and 3.

Bimodal and multimodal polygons have received so much attention in the literature of variation that the interest of a more detailed investigation was at once apparent. Before considering further our data on this species we may note the more important discussion of these anomalous frequency distributions.

TABLE I

TOTAL LAMINÆ AND TOTAL FLOWERS PER INFLORESCENCE

Laminæ per Inflorescence.	Flowers per Inflorescence 1	2	3	4	Totals.
1	1	—	—	—	1
2	1	—	—	—	1
3	4	1	1	—	6
4	38	25	47	—	110
5	9	18	28	—	55
6	36	22	158	2	218
7	1	1	2	4	8
8	—	—	—	1	1
Totals.	90	69	236	7	400

Bateson[4] gives a bimodal variation polygon for the length of horns in the beetle *Xylotrupes gideon* and the length of the forceps in the earwig, *Forficula auricularia*, but the factors underlying the phenomena are not demonstrated. Naturally the first suggestion concerning a bimodal or polymodal polygon is that there is taxonomic heterogeneity in the material examined. Davenport and Blankenship[5] have even suggested criteria for determining whether the component elements of a two-humped curve are to be designated as "varieties" or "species." So far as I am aware the first attempt to analyze a bimodal polygon into its component elements is that of De Vries[6]

[4] Bateson, W., "Materials for the Study of Variation," pp. 37–42, fig. 2–3, 1894.

[5] Davenport, C. B., and J. W. Blankinship, *Science*, N. S., Vol. VII, pp. 685–694, 1898.

[6] De Vries, H., *Archiv für Entwickelungsemechanik*, Vol. II, 1895; also *Ber. Deutsch. Bot. Ges.*, Vol. XVII, pp. 84–98, 1899; also "Die Mutationstheorie," Vol. I, pp. 526–529; Vol. II, p. 349.

with *Chrysanthemum segetum*. Pearson[7] in the first of his "Mathematical Contributions to the Theory of Evolution" deals with the mathematical analysis of composite frequency curves.

Dimorphism referable to peculiar environmental conditions has received considerable attention, but unfortunately quantitative data are not numerous. For seasonal dimorphism in Idotheca, Gadzikiewicz[8] has published some figures which yield very different polygons for the body length of September and March females.

The above cases are illustrative merely and make no pretense at completely setting forth the literature.

Ludwig and his pupils have devoted a whole series of papers[9] to the discussion of multimodal variation polygons. De Vries in "Die Mutationstheorie" lays considerable stress upon the Fibonacci series. More recently Ritter[10] and Heyer[11] have taken up the questions and the reader should consult these papers for a full statement of the problems and the pertinent literature. In any discussions in this field, the warnings set forth in papers by Pearson[12] and by Pearson, Yule, Tower and Lee[13] on the sources of apparent polymorphism in plants should always be kept clearly in mind.

Here I do not care to discuss the work of those who conclude that frequency curves have modes where they

[7] Pearson, K., *Phil. Trans. Roy. Soc. Lond.*, A., Vol. CLXXXV, pp. 71–110.

[8] Gadzikiewicz, *Bull. Acad. Sci. St. Petersb.*, Vol. XXIV, pp. 263–272, 1906; also *Biolog. Centralbl.*, Vol. XXVII, pp. 505–508, 1907.

[9] A complete bibliography of this work is quite out of place here. The reader may consult F. Ludwig, *Biometrika*, Vol. I, pp. 11–29, 1901, for a general statement of some of Ludwig's own views. See also citations by Ritter.

[10] Ritter, G., *Beih. Bot. Centralbl.*, Abth. II, Vol. XXII, pp. 317–330, 1907; Abth. I, Vol. XXIII, pp. 273–319, 1908; Abth. I, Vol. XXV, pp. 1–29, 1909. Rather full citations of the literature are given in these papers.

[11] Heyer, A., *Biometrika*, Vol. VI, pp. 354–365, 1909.

[12] Pearson, K., *Biometrika*, Vol. I, pp. 260–261, 1902.

[13] Pearson, K., G. U. Yule, W. Tower and A. Lee, *Biometrika*, Vol. 1, pp. 304–319, 1902. See also a note on a paper by Shull, *Biometrika*, Vol. 11, pp. 113–114, 1902.

would be expected in accordance with some mathematical series. It is obvious to any one trained in working with numbers that there are serious difficulties in the way of demonstrating a number of modes in a frequency distribution. The errors of random sampling can not be disregarded and when the variation is continuous instead of discrete the chances of errors due to biased judgment are great. These facts emphasize the necessity for seeking out the simplest possible cases of polymorphism and determining in so far as possible the morphological conditions which underlie them. Such a case seems to be offered by the involucral leaves of Syndesmon.

After I had made my first series of countings a paper by Kellerman[14] giving the essential morphological features of the leaves and considerable statistical data concerning their variation came to my notice. He does not present his data in a form suitable for statistical consideration, and did not note the bimodal condition which appears where a curve is plotted for the entire number of laminæ.

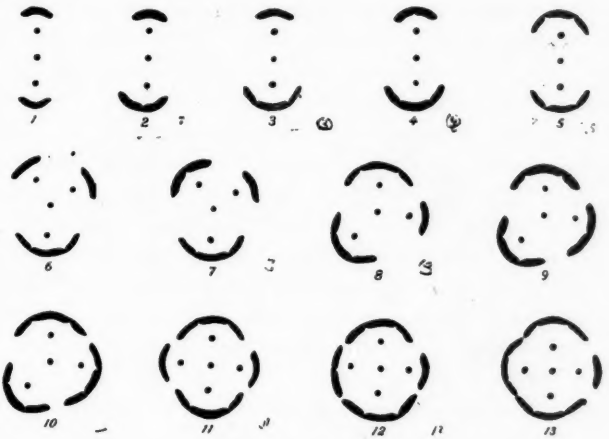
Kellerman's diagrams represent the morphology of the inflorescence very well and are reproduced here with such additional ones as are necessary to represent the types of leaves observed in our series. The terminal and axillary buds which may develop into flower-bearing axes are represented by solid dots. The number of leaflets into which a leaf is divided is indicated by the partial division of the line representing the leaf. Unfortunately Kellerman's data are rather too few to be given further statistical analysis. For figures illustrating the general appearance of different inflorescences the reader may consult his plate.

Most simply the inflorescence consists of a terminal flower, two involucral leaves and two axillary flowers. The axillary buds do not always develop. The leaves may be entire or divided into (generally) three leaflets.

The form of inflorescences with two leaves, one ter-

[14] Kellerman, W. A., *Ohio Nat.*, Vol. I, pp. 107–110, 1901.

minal flower and two axillary flowers is shown in Figs. 1 to 5. In our series we find all cases from those with both leaves simple to those with both leaves ternately compound.



Inflorescences of Seq.

In the next group of inflorescences an extra leaf is added. The additional axillary bud thus introduced raises the normal number of pedicels to four. Among the inflorescences with a whorl of three leaves I found none in which at least one of the leaves was not ternately com-

TABLE II

FREQUENCY OF DIFFERENT TYPES OF INFLORESCENCES WITH 2 LEAVES

Class.	*f*	Class.	*f*
1—1—**3** (3)	1	3—2—**3** (3)	13
1—1—**3** (2)	0	3—2—**3** (2)	7
1—1—**3** (1)	1	3—2—**3** (1)	11
Fig. 1		Fig. 4	
2—1—**3** (3	0	3—3—**3** (3)[15]	297
2—1—**3** (2)	2	3—3—**3** (2)	95
2—1—**3** (1)	1	3—3—**3** (1)	74
Fig. 2		Fig. 5	
3—1—**3** (3)	9	Total.	544
3—1—**3** (2)	16		
3—1—**3** (1)	17		
Fig. 3			

pound, but in three of them two of the leaves were simple. The different normal types observed are made clear by diagrams 6 to 10.

TABLE III

FREQUENCY OF DIFFERENT TYPES OF INFLORESCENCES WITH 3 AND 4 LEAVES

Class.	*f*	Class.	
3—1—1—4 (4)	2	3—3—2—4 (5)[18]	1
3—1—1—4 (3)	1	3—3—2—4 (4)	4
3—1—1—4 (2)	0	3—3—2—4 (3)	0
3—1—1—4 (1)	0	3—3—2—4 (2)	1
Fig. 6		3—3—2—4 (1)	0
3—2—1—4 (4)	1	Fig. 9	
3—2—1—4 (3)	0	3—3—3—4 (4)	6
3—2—1—4 (2)	0	3—3—3—4 (3)	2
3—2—1—4 (1)	1	3—3—3—4 (2)	0
Fig. 7		3—3—3—4 (1)	0
3—3—1—4 (5)[16]	3	Fig. 10	
3—3—1—4 (4)[17]	76	Total.	137
3—3—1—4 (3)	15		
3—3—1—4 (2)	7	3—3—1—1—5 (5)	1
3—3—1—4 (1)	17	3—3—1—1—5 (3)	1
Fig. 8		Fig. 11	
		3—3—2—1—5 (5)	1
		Fig. 12.	
		3—3—3—1—5 (3)	1
		Fig. 13	
		Total.	4

Finally, four leaves with the possibility of four axillary pedicels may be found. The condition of the division of these leaves into leaflets is shown in Figs. 11 to 13.

[15] We may note four slightly abnormal inflorescences of the 3—3—3 type. In one there was concrescence of the terminal and one axillary pedicel for some distance from the base. In another one of the axillary peduncles bore a lateral leaf. In a third the central of the three leaflets of one of the leaves was again divided into three secondary leaflets. In the fourth case the two leaves were not opposite, as is usually the case, but were considerably separated on the axis.

[16] In one of these three cases two peduncles are produced from one of the axils. In the other two, one of the axillary pedicels bears a leaf subtending a secondary pedicel bearing the fifth fruit.

[17] In one of these 76 cases the fourth flower is due to one of the lateral pedicels bearing a leaf in the axil of which a secondary pedicel is borne; one of the axillary buds produces no flower in this case. In two other cases one of the axillary pedicels bore a leaf, but no pedicel was produced in its axil. In one of these cases one of the three leaflets—a lateral one—was again divided into two secondary leaflets.

[18] The fifth flower is due to two axillary pedicels being produced from one of the leaves.

Certain "teratological" cases are not represented by figures, but are described merely.

We may now turn to the important question of the frequency of the several morphological types in the Cold Spring Harbor collection made in the spring of 1909.

In classifying these inflorescences all which were injured in any way so that the number of primary divisions of the leaf could not be made out with certainty were discarded. Especial care was used in cases in which a leaf was apparently divided into two leaflets, since such often results from the breaking off of one of the lateral leaflets of a ternately compound leaf. In some cases inflorescences were included in which the laminæ of the primary leaflets were not intact, so that the data can not be trusted for the frequency of secondary divisions. In counting, only completely divided laminæ were considered as leaflets.

Petiolate leaves were not infrequently found, but no special record was kept of them.

The data are set forth in minutely analyzed form in Table II–III. The light-faced numbers separated by dashes represent the number of primary leaflets into which the leaves are divided. The black-faced numbers show the number of flower-buds—terminal and axillary—which might normally have developed, and the number immediately following in parentheses shows the number actually developing. The *f* (= frequency) column gives the number of occurrences of each type.

Grouping the data according to the number of leaves per inflorescence, we find:

Two leaves, in 544 cases.
Three leaves, in 137 cases.
Four leaves, in 4 cases.
685 altogether.

Here is an example of what De Vries[19] has termed a half-Galton curve. Whether it would be possible to increase the number of leaves by selection as De Vries was

[19] De Vries, H., *Ber. Deutsch. Bot. Ges.*, Vol. XII, pp. 197–207, 1894.

able to do in the case of the petals of Ranunculus could only be determined by direct experiment. Possibly the skew curve here found is merely due to the age or vigor of the individuals.

Considering next the distribution of the number of primary leaflets per leaf in the material we may seriate the number of leaflets for each class of plants separately, as in Table IV.

TABLE IV

NUMBER OF PRIMARY LEAFLETS PER LEAF IN LEAVES FROM ALL DIFFERENT CLASSES OF INFLORESCENCES

Lobes per Leaf.	Leaves per Inflorescence: 2	3	4	Totals.
1	49	126	6	181
2	34	8	1	43
3	1005	277	9	1291
Totals.	1088	411	16	1515

Only sixteen leaves were available for the inflorescences producing four leaves, but for those with two and three leaves the number is ample. In each of the three classes of inflorescences, and in the total, there is a pronounced mode on undivided leaves and on those with three leaflets. Throughout, those with two leaflets are much less frequent than those with either one or three.

Reducing the frequencies for the inflorescences with two and three leaves to a percentage basis for more direct comparison, and laying them side by side in Figs. 14 and 15, we note at once that there is a wide difference in the proportion of single leaves in the two series. The source of this difference is at once clear. In the inflorescences with the third leaf, the additional leaf is nearly always simple. Thus the proportion springs at once from about 4.5 per cent. to 30.5 per cent.

Unfortunately, our data, though extensive, are not numerous enough to permit of further analysis. If material were more ample it might be possible to ascertain more precisely some of the factors determining the con-

dition of division of the leaf. All that we can conclude from the present data is that: (*a*) There is a strong tendency to the production of either simple or ternately com-

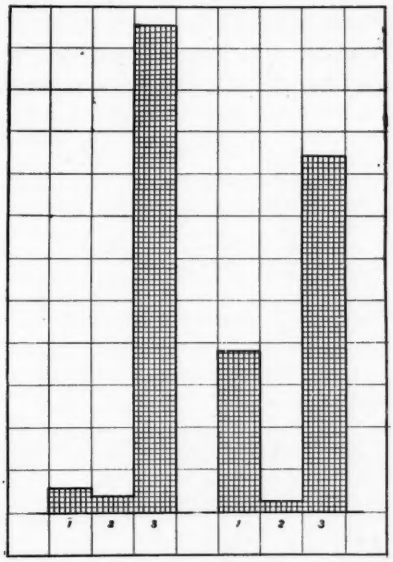


FIG. 14. FIG. 15.

pound leaves—those divided into two leaflets are rare; (*b*) a larger proportion of the leaves are simple in inflorescences with three or four leaves than in those with but two leaves.

To determine whether the distribution for number of leaf laminæ per involucre in this series forms a bimodal distribution similar to that found in 1905, I extract the totals from the two tables of data. To ascertain more accurately the real source of the bimodal condition, should it be found to exist in this series, the combinations which give rise to the different total numbers are given in Table V.

From these figures appear several points which could not be determined at all on the lumped data as collected in 1905.

The grand total shows that there is a slight empirical mode on four and a conspicuous one on six laminæ, as compared with the very prominent modes on these two grades in 1905. The distributions from the three classes of inflorescences shows the origin of these modes very clearly. The mode on four is due entirely to the tendency to the production of one ternately compound and one simple leaf. Both of these types of leaves have been shown to be much more frequent than those divided into two leaflets. The mode on six is due to both of the involucral leaves bearing the modal (three) number of leaflets.

TABLE V

SHOWING THE FREQUENCY AND MODE OF ORIGIN OF THE DIFFERENT TOTAL NUMBERS OF LAMINÆ PER INFLORESCENCE

Total Laminæ per Inflorescence.	Laminæ of Individual Leaves																
	Two Leaves.						Three Leaves						Four Leaves.				Grand Totals.
	1—1	2—1	3—1	3—2	3—3	Totals.	3—1—1	3—2—1	3—3—1	3—3—2	3—3—3	Totals.	3—3—1—1	3—3—2—1	3—3—3—1	Totals.	
2	2					2											2
3		3				3											3
4			42			42											42
5				31		31	3					3					34
6					466	466		2				2					468
7									118			118					118
8										6		6	2			2	8
9											8	8		1		1	9
10															1	1	1
	2	3	42	31	466	544	3	2	118	6	8	137	2	1	1	4	685

In the 1905 series inflorescences with seven leaflets formed only 2 per cent. of the population; in the 1909 lot they are over 17 per cent. of the total number. There is no way of determining absolutely why there is such a difference, but it seems quite logical to suppose that in the Cold Spring Harbor series inflorescences with three leaves were much more abundant than in the Meramec Highlands lot, for the frequency of seven laminæ in the Cold Spring Harbor material is entirely due to flowering stalks with three leaves of which two are ternately compound and the third undivided.

In the 1905 series all the laminæ found in the inflorescence were included in the countings. In the discussions just given I have treated only the primary leaflets. The data for the other laminæ are included in the notes on the tables of data or in the notes on teratological cases. Their addition would make little difference in our distributions, but the data are available for any one who cares to use them.

TABLE VI

SERIATION OF NUMBER OF FLOWERS DEVELOPING IN DIFFERENT TYPES OF INFLORESCENCES

Flowers per Inflorescence.	Leaves per Inflorescence 2	3	4	Totals.
1	104	18	—	122
2	120	8	—	128
3	320	18	2	340
4	—	89	—	89
5	—	4	2	6
	544	137	4	685

Further analysis of the data for leaf characters is not justified by the quantity of material. Two conclusions are seen to be amply justified by the facts: (*a*) In Syndesmon there is a strong tendency to the production of simple and trifoliate leaves. (*b*) The preceding fact, taken in connection with the peculiarities of the inflorescence with regard to the number of leaves produced, is quite sufficient to account for the bimodal condition of the variation polygon for number of laminæ per inflorescence.

The bimodal polygon is therefore explicable on purely morphological grounds without any assumption of the mixture of two or more "races" or "minor species," provided the plants producing two, three and four leaves per inflorescence be not considered "small species" or "biotypes." Personally I see no reason whatever to think that they are, but in these days of minute segregation the possibility must not be left unmentioned. To me it seems not unlikely that the three different classes of

inflorescences noted are to some extent to be referred to age differences in the individuals producing them.

The number of flowers developing may now be tabulated for each of the three classes of inflorescences. The results are given in Table VI.

Here the bimodal condition in the number of flowers per inflorescence found in the 1905 series does not appear, although the frequency of inflorescences with one flower is about as great as that of those with two. Doubtless the reason for this difference would be clear if we had as complete information concerning the 1905 series as is available for the 1909 material.

The purpose of the present note will have been fulfilled if in addition to the recording of a mass of definite quantitative data concerning the form of the inflorescence in Syndesmon, it convinces students of variation of the importance of a critical consideration of purely morphological features before concluding that an empirical multimodal polygon indicates the existence of biotypes.

COLD SPRING HARBOR, L. I.

THE MIOCENE TREES OF THE ROCKY MOUNTAINS

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THE living arborescent flora of the Rocky Mountain region is at the present time occupying the attention of a number of able workers, including Nelson in Wyoming, Rydberg of the New York Botanical Garden, Sudworth of the Forest Service, Ramaley, Bethel and Schneider in Colorado, Wooton in New Mexico, and others. As a result of all this activity, we are promised two manuals of Rocky Mountain botany, and a third of trees alone, so we shall have three separate and independent treatments of our woody flora to compare and choose from.

Unfortunately, those who have been so active and exhaustive in their investigations of the living flora have not cared, as a rule, to consider the historical or paleobotanical side of the subject. Many "recent" botanists seem to have a positive dislike for fossil plants, and few manifest any great eagerness to receive information about the ancestors or predecessors of the species which occupy their attention. Like all enthusiasts, the writer is filled with the idea that the matter has only to be adequately presented to command universal attention; and hence offers this discussion, not so much for the paleobotanists as for those students of living plants whose active interest may be aroused in the problems involved.

Going back from the present time, we are practically without information concerning the plants of our region until we come to the Florissant beds, assigned to the Miocene. These beds, however, contain an abundant series of remains, many of the plants beautifully preserved, as the accompanying illustrations show. They testify to a climate both warmer and damper than that of the present day, the arborescent genera including Sapindus, Ficus,[1] Diospyros, Persea, Leucæna, Anona,

[1] The determination of *Ficus* is based on the leaves. In confirmation of

etc., but so far as known no palms. Some, as *Ailanthus americana,* pertain to genera now restricted to Asia.

The determination of the age of the Florissant beds has been a matter of some difficulty, notwithstanding the large number of organisms preserved. Comparing the flora with that of the European Tertiary, I have felt satisfied that it should be referred to the Miocene, and probably to the Upper Miocene. The resemblance to the flora of Œningen in Baden, known to be upper Miocene, is most striking. Thus we have the following parallel or representative species:

Florissant.	*Œningen.*
Liquidambar convexum Ckll.	*Liquidambar europæum* A. Br.
Ulmus braunii Heer, Lx.	*Ulmus braunii* Heer.
Comptonia insignis (Lx.) Ckll.	*Comptonia œningensis* A. Br.
Porana speirii Lx.	*Porana œningensis* A. Br.
Porana tenuis Lx.	*Porana macrantha* Heer.
Acer florissanti Kirch.	*Acer tricuspidatum* A. Br.[2]

Many others could be cited. On the other hand, the Florissant incense cedar, *Heyderia* or *Libocedrus coloradensis* Ckll., is to be compared with *H. salicornioides,* of the Lower Miocene of Radoboj in Croatia. The Florissant redwood, *Sequoia haydeni* (Lx.), is not related to *S. sternbergi* Heer from Œningen, but to *S. langsdorfii* (Brgt.) Heer of the Swiss Lower Miocene; this species, however, survived into the Upper Miocene in Italy and Galicia. This *S. langsdorfii* has been recognized in America also from the Upper Cretaceous to the Miocene, and some of the Florissant specimens have been referred to it; but the identity of the plants from so many diverse localities and horizons is questionable, and from Florissant I think we have only one species, *S. haydeni.*

The Sequoia and Libocedrus of Florissant are both very closely related to their living Californian allies; so

it comes a discovery by Mr. Brues, who in working over the parasitic Hymenoptera from Florissant has come upon what appears to be a genuine fig-insect, apparently of the South American genus *Tetrapus* Mayr.

[2] *Acer trilobatum* (Sternb., 1825) A. Br., 1845; not *A. trilobatum* Lam., 1786.

much so that one is in some difficulty to point out any tangible differences. This is equally true of a number of other cases, of which the following are illustrative:

Florissant.	*Living.*
Pinus wheeleri Ckll.	*Pinus flexilis* James.
Pinus sturgisi Ckll.	*Pinus tæda* L.
Ailanthus americana Ckll.	*Ailanthus glandulosa* L.
Sambucus newtoni Ckll.	*Sambucus arborescens* Nutt.
Anona spoliata Ckll.	*Anona glabra* L.
Robinia brittoni Ckll.	*Robinia pseudacacia* L.
Populus lesquereuxi Ckll.	*Populus angustifolia* James.
Quercus lyratiformis Ckll.	*Quercus lyrata* Walt.
Sapindus coloradensis Ckll.	*Sapindus drummondi* H. & A.

So numerous are the resemblances to the living flora that one might well feel persuaded to refer the beds to the Pliocene—certainly better there than to the Oligocene or Eocene! However, the Florissant fishes, with the exception of Amia, are of extinct genera, and no less than 178 genera of insects are supposed to be extinct. For a variety of reasons, based chiefly upon a study of the insects, I believe that the Florissant period corresponds with Osborn's "Fifth Faunal Phase" (Bull. 361, U. S. Geol. Survey), in which a new fauna was invading the country from Eurasia, while connection with South America had not yet been established. Some of the Florissant groups of insects, such as the Aphididæ and Bombyliidæ, seem to represent the original American fauna uncontaminated; while others show old world types, the most significant and interesting of which is the tsetse fly (*Glossina*).[3] Osborn's "Fifth Phase" includes the Middle and Upper Miocene, and so far as may be judged, Florissant should belong near the middle of it.

The attempt to correlate the Florissant beds with other American floras ascribed to the Miocene brought out a number of difficulties. With the exception of the little-

[3] A second species of tsetse fly, *Glossina osborni* Ckll., has been recently discovered. It is only 10½ mm. long, the wing 7 mm.; the venation is normal for the genus, but the first basal cell bulges less subapically than in Scudder's species.

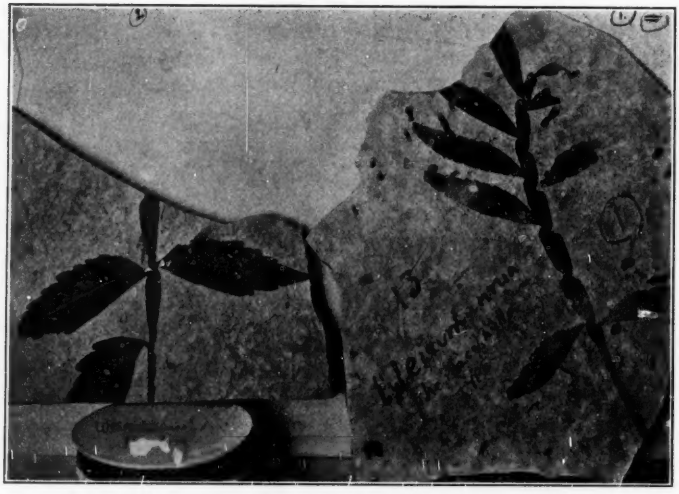

FIG. 2. *Weinmannia lesquereuxi* Ckll. FIG. 1. *Weinmannia phenacophylla* Ckll.

known formation at Elko Station, Nevada, I do not find anything which really seems to correspond with Florissant. According to the theory outlined above the Mascall beds of Oregon, which possess a varied flora, should be either contemporaneous or (more probably) somewhat earlier. Fortunately, fourteen species of mammals have been obtained from the Mascall, and these place it rather definitely in the Middle Miocene. Considering, therefore, a probable moderate difference in time, combined with noteworthy geographical and altitudinal differences, we ought to find the Mascall flora similar to, but by no means identical with, that of Florissant; and this is exactly what comparisons show.

Thus of the 77 Mascall plants (nearly all trees) referred to definite genera, no less than 56 are congeneric with those of Florissant. Of those not congeneric, five are so dubious that they have not been specifically determined. The Mascall genera not yet found at Florissant are the following:

1. *Equisetum.*—This has no significance, as it abounds in Colorado to-day, and must have been present during the Florissant period.

2. *Ginkgo.*—Represented in the Mascall by a fragment not specifically determined. This genus is not known in the Rocky Mountains later than the Laramie and Livingston, on the border line between the Cretaceous and Tertiary. As is well known, there is a single living (Asiatic) species.

3. *Thuites.*—A fragment not specifically determined. It is practically identical with *T. ehrenswärdi* Heer (Miocene of Sachalin and Spitzbergen), but that plant appears to be referable to the modern genus Chamæcyparis.

4. *Glyptostrobus.*—A genus still living in China. It was supposed to occur at Florissant, but I believe the material so referred all belongs to Sequoia. The Mascall material is not above suspicion of also being Sequoia; indeed Lesquereux so referred one of the specimens.

5. *Taxodium.*—The Mascall specimens are referred by Knowlton to the widely distributed *T. distichum miocenum* Heer, which should be called *Taxodium distichum dubium* = *Taxodium dubium* (Sternb.) Heer, originally described from Bilin. This differs from Sequoia by the deciduous leaves, which are not decurrent at the base as in Glyptostrobus. The genus still lives in our southern states.

6. *Artocarpus.*—Represented by very fragmentary material, doubtfully referred to *A. californica* Kn.

7. *Magnolia.*—Major Bendire collected a plant which Knowlton says "may well be" *M. inglefieldi* Heer. It has not been obtained by recent collectors. *Magnolia dayana* Ckll. ined. (*M. lanceolata* Lx. 1878, not Link. 1831) is listed by Knowlton as from the Mascall, but in his detailed account he says it is from Cherry Creek, which should be Lower Eocene.

8. *Laurus.*—Florissant has a species of Persea; Laurus and Persea are allied, and not distinctly separated by paleobotanists.

9. *Platanus.*—The Mascall specimens appear to belong

FIG. 3. *Sequoia haydeni* (Lesquereux). Redwood.

to three species, but none are sufficiently well preserved for positive specific identification.

10. *Prunus.*—The two Mascall species described by Knowlton are only doubtfully referred to this genus, which is of course abundant in the modern flora.

11. *Rulac.*—Generic reference rather uncertain; the genus is scarcely separable from Acer, which occurs at Florissant.

12. *Æsculus.*—This well-known living genus is repre-

sented in the Mascall by leaflets which closely resemble an undescribed Florissant species which may be a Berberis, but is certainly not an Æsculus.

13. *Grewia.*—The Mascall plant is referred by Knowlton to *G. crenata* (Unger) Heer, which occurs in Europe at Œningen.[4]

Three other genera, Phragmites, Cyperacites and Smilax, are non-arborescent, and have no particular significance.

Thus it would appear that in the Middle Miocene period Ginkgo and Glyptostrobus—if we may accept the determinations—had not yet retreated from the American continent, but survived at least in the northwest. For the rest, the Mascall flora is no doubt a lowland one as compared with that of Florissant, and this alone would explain many of the differences; thus, no one would expect to find Taxodium growing around a mountain lake.

Dr. Knowlton has described (Monog. U. S. Geol. Survey, Vol. 32, part 2) an extensive flora from the Yellowstone, which he regards as Miocene. The fossil plants of the Yellowstone National Park are divided by him into three series: (1) Fort Union, which is Basal Eocene, (2) Intermediate, said to be Miocene, and (3) Lamar Flora, also Miocene. With the first we are not now concerned, but the others must be compared with the flora of Florissant. Considering the relative proximity of the Yellowstone beds to those of Colorado, one would expect to find much similarity and even identity in the plants; but this is not the case. The difference of locality, with a moderate difference in time, might perhaps account for the diversity of species; but the Yellowstone flora as a whole does not impress one as being so modern as that of the Mascall beds or Florissant, while there is a significant *identity of species* with those of the Eocene.

I have extracted from Knowlton's tables a list of all the Yellowstone "Miocene" plants said to occur elsewhere or in the Eocene, with the following result:

[4] The African *Grewia crenata* Hochst., 1868 (not Unger, 1850), takes the name *G. populifolia* Vahl, 1790.

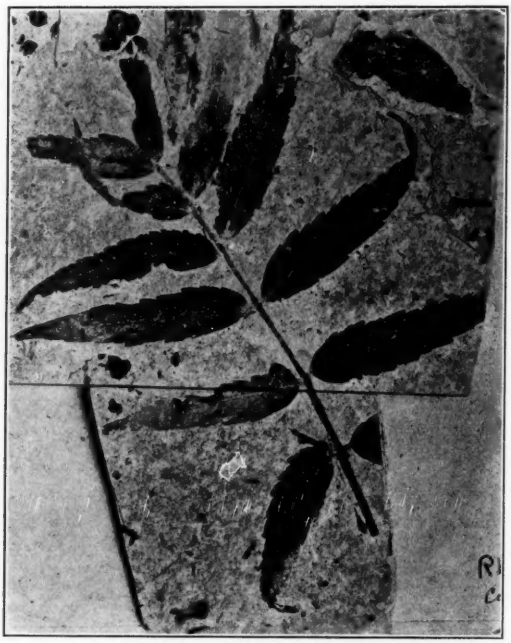

FIG. 4. *Rhus coriarioides* Lesquereux. Sumach.

1. Common to Fort Union (Eocene), Intermediate and Lamar.

Sequoia langsdorfii (Brgt.). Said to go down to the Laramie (Cretaceous).

Juglans rugosa Lx. Goes down to the Laramie.

Castanea pulchella Kn.

Ficus densifolia Kn.

Laurus californica Lx. Also auriferous gravels of California.

Laurus grandis Lx. (not Wallich). Also auriferous gravels of California.

Platanus guillelmæ Göpp. Perhaps also Laramie.

Aralia notata Lx. Also Denver beds.

* *Elæodendron polymorphum* Ward.

2. Common to Fort Union and Intermediate.

Equisetum canaliculatum Kn. Perhaps also in the Lamar.

Magnolia (?) *pollardi* Kn.
* *Ulmus minima* Ward?
Sapindus affinis Newby.

3. Common to Fort Union and Lamar.
Asplenium iddingsi Kn.
Lygodium kaulfussi Heer.
Equisetum deciduum Kn.
Juglans crescentia Kn.
Ficus asiminæfolia Lx. Also auriferous gravels of California.
Laurus primigenia Unger?
Malapœnna lamarensis Kn.
Sapindus grandifoliolus Ward.
Sapindus wardii Kn.
* *Hicoria antiqua* (Newb.).
**Ulmus pseudofulva* Lx.?

Those marked with an asterisk occur in the Fort Union only outside of the Yellowstone.

4. Common to the Intermediate and the Denver beds (Basal Eocene).
Osmunda affinis Lx.

5. Common to the Lamar, Basal Eocene and Laramie.
Rhamnus rectinervis Heer, Lx. Heer describes this from Monod, in the Lower Miocene; we may venture to doubt the identity of the American plant.

Thus we have twenty-six plants *specifically* identical with those of the Basal Eocene.[5]

6. Common to Lamar and "Green River" of Knowlton. (See also under 7.)
Salix elongata O. Web. Said to occur at Elko Station, Nevada, but represented only by uncharacteristic fragments. The determination of

[5] The Mascall is supposed to have five species common to the Fort Union; but of these two are doubtful, two others are the conifers *Sequoia langsdorfii* and *Taxodium*, while the fifth is *Sapindus obtusifolius*, to which a single specimen from the Mascall "seems to belong." *S. obtusifolius* was originally described from beds supposed to belong to the Washakie (Later Eocene).

FIG. 5. *Ulmus hilliæ* Lesquereux. Elm.

the Lamar plant is considered doubtful by Knowlton.

Fagus (*Fagopsis*) *longifolia* (LX.). Elko Station, Nevada; Florissant (very abundant) and Eocene (?) of British Columbia. The British Columbia locality is on the Similkameen River, whence come various fossil insects. Dr. Dawson (quoted by Scudder) considered these deposits Miocene. The Yellowstone collection includes about forty specimens which Knowlton

refers here, all from Fossil Forest Ridge. This is, undoubtedly, a distinctively Miocene plant, and must be accepted as pertinent evidence. The determination must be presumed to be correct, though it may be pointed out that various other leaves have almost exactly the same venation and appearance. This is especially true of the species of Zelkova, to which genus Engler (1894) actually referred *F. longifolia,* though the discovery of the fruit has since shown that it is not related thereto. *Ulmus plurinervia,* as figured by Heer from Alaska, is also almost exactly like *F. longifolia;* it is considered doubtfully Eocene, but Knowlton has recognized it in the Mascall (Miocene). From the shape of the base, and other features, it seems to me certain that the Alaskan plant is not the original *U. plurinervia,* of which Unger gives four figures in the Chloris Protogæa. The latter is decidedly more elm-like in appearance.

Corylus macquarrii (Forbes) Heer. This plant, as recognized in America, is a Fort Union and possibly Laramie species; recorded also from the Eocene (?) of Alaska.

Diospyros brachysepala A. Br. As recognized in this country, this is a Laramie and Fort Union species; the record from Florissant I believe to be erroneous.

None of the above belong to the genuine Green River series; three are quite without significance as indicating Miocene affinities, but the *Fagus* stands out as a solitary Miocene representative.

7. Common to the Lamar and the Auriferous gravels of California. (See also under 1 and 3.)

Juglans leonis Ckll. Two specimens in the Lamar.

Populus balsamoides Göpp. Also Miocene (?) of Alaska. Known in the Yellowstone only from a fragment, which certainly can not be positively determined as *balsamoides:* in fact, it shows

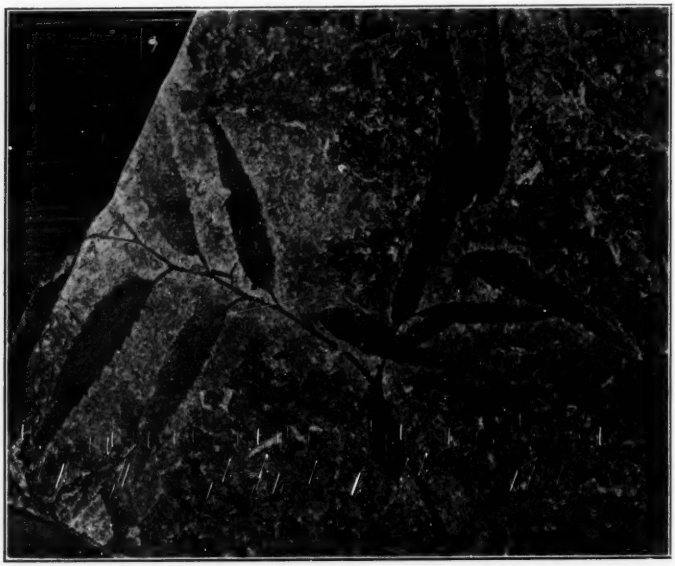

FIG. 6. *Myrica drymeja* (Lesquereux).

some differences, at least as compared with the original European *balsamoides,* which ought to be specific.

Salix varians Göpp. Eocene (?) of Alaska. The Lamar plant is a fragment, and according to the figure, the margin is quite unlike that of the European *varians.*

Salix angusta A. B. Said to occur also in the Basal Eocene and true Green River. The Lamar material consists of doubtful fragments.

Quercus furcinervis americana Kn.

Ficus shastensis Lx.?

Ficus sordida Lx. A mere fragment from the Lamar.

Ficus asiminæfolia Lx. Very indifferent material from the Lamar. Also Fort Union.

Magnolia californica Lx.? The Lamar plant is represented by a single specimen, "so much

broken that its positive identification is not possible" (Knowlton).

Persea pseudocarolinensis Lx. The Lamar specimen figured, "the best one found," consists of the upper half of a leaf; what there is of it appears to agree with the Californian species, although it has more lateral viens.

Rhus mixta Lx.?

Aralia whitneyi Lx. Also in the Intermediate. None of the Yellowstone specimens are perfect, but they appear to belong to this handsome species.

Thus the species common to the Lamar and Auriferous gravels, *but not known from Basal Eocene*, are few, and in several cases of doubtful identity. As the reference of the Lamar to the Miocene rests wholly on the resemblance of the flora to that of the Auriferous gravels, with the exception of the indication afforded by *Fagus longifolia*, it must be considered at least somewhat dubious. It is also to be remarked that eleven species of plants are supposed to be common to the Yellowstone Fort Union and the Auriferous gravels, although two of these, at least, are doubtfully from the gravels, while in four or five cases the Yellowstone material is fragmentary or doubtful.

It is one thing, however, to recognize distinct elements in common between the Auriferous gravels and the Lamar, and another to prove the latter Miocene thereby. The former may be conceded, the latter I think not.

Lesquereux enumerates thirteen species from the Auriferous gravels which are almost identical with living species; he also cites seventeen which are evidently, but not very closely, related to living ones. Of the thirteen, four are enumerated from the Lamar; of the seventeen, not one. Of the four common to the Lamar, three are dubious, and only *Juglans leonis* (a species represented to-day by the Asiatic *J. regia*) appears to be of satisfactory standing.

FIG. 7. *Populus crassa* (Lesquereux). Cottonwood; probably fruit of *P. lesquereuxi*.
FIG. 8. *Populus lesquereuxi* Ckll. Cottonwood.

Four species of the Auriferous gravels are said by Lesquereux to be identical with Miocene plants, but are all unsatisfactory, as follows: (1) *Fagus antipofii;* perhaps goes to the Laramie, and the Californian specimen was only half a leaf. (2) *Populus zaddachi;* supposed to go down to the Basal Eocene. (3) *Ficus tiliæfolia;*[6]

FIG. 9. *Salix ramaleyi* Ckll. Willow.

[6] *Ficus tiliæfolia* (A. Br.) Heer, 1856, has priority over *F. tiliæfolia* Baker, Jn. Linn. Soc. **21**: 443 (1885), from Madagascar. The latter may become *Ficus bakeriana* n. n.

said to go down to the Laramie. (4) *Aralia zaddachi;* of uncertain determination, one of the specimens was *Platanus dissecta.* None of these is found in the Lamar, but *F. antipofii* is in the Yellowstone Fort Union.

Eight other species from the Auriferous gravels are stated to be allied to Miocene species, five of these being also related to living plants. One of the five, *Juglans oregoniana,* has since proved to be from the Mascall, and not to occur in the Auriferous gravels. The other three are as follows:

Ficus sordida Lx. Allied to, or perhaps identical with, *F. grœnlandica* of Greenland. A fragment referred to this has been found in the Lamar.

Ficus mengæ n. n. (*F. microphylla* Lx., 1878, not Salzm., Mart. Fl. Braz. 4: 93). Allied to *F. planicostata*—but this is a species of the Basal Eocene and Laramie.

Aralia whitneyi Lx., said to be allied to an Evanston species, which would be Eocene.

It is thus apparent that the Auriferous gravels flora has no decisive Miocene affinities, but is composed of two sets of plants, one related to living forms, the other to those of the Eocene. It is known to be a mixed lot, and when I recently suggested to Dr. J. C. Merriam, of the University of California, that it might perhaps be partly Pliocene and partly Eocene, he replied that this might indeed be the case.

It is further to be remarked that Knowlton formerly regarded the Mascall flora as having affinity with that of the Auriferous gravels; but he subsequently discovered that certain of the species he had most relied on were really confined to the Mascall, and did not occur in the gravels at all. "This correlation therefore fails," he states, and the absence of relationship stands as an argument against the Miocene age of the gravels.

The conclusion seems to be legitimate that the Yellowstone Intermediate and Lamar floræ are Upper Eocene, or at least older than Miocene. Were they really Mio-

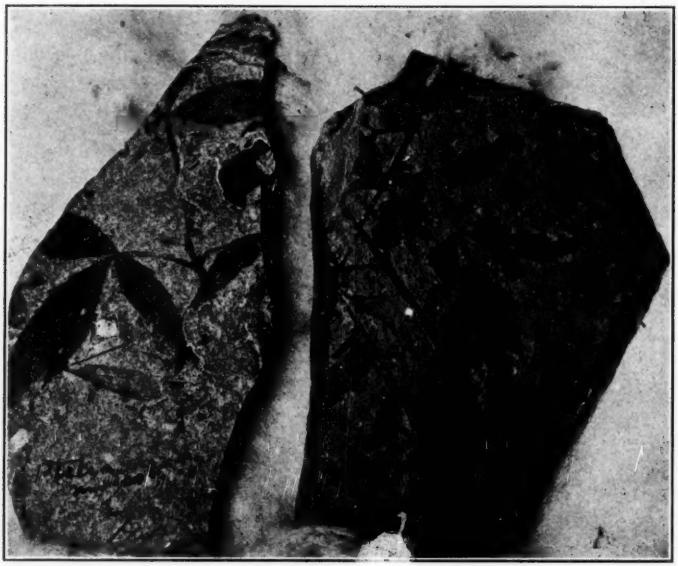

FIG. 10. *Ptelea modesta* (Lesquereux). FIG. 11. *Melia expulsa* Ckll.

cene, with so much resemblance to even the Basal Eocene, the Florissant flora, to get as far on the other side as its lack of affinity would suggest, would have to be projected somewhere into the future! If this opinion is in any degree correct, Florissant remains as the only Rocky Mountain locality for Miocene plants, so far as known.

The accompanying figures, all taken from specimens obtained at Florissant by the University of Colorado expeditions, will give a good idea of the material from that locality. Nowhere else in America are Tertiary plants so well preserved. As compared with the Eocene flora, and especially the Basal Eocene, the Florissant trees are more diverse in type, with usually smaller leaves, which are often compound. Excessively moist conditions are not indicated, though there was evidently much more moisture than at the present day. Some of the plants are even somewhat xerophytic, indicating that the higher slopes may have been relatively dry. Osborn remarks on the evidence of increasing summer droughts

in the Middle Miocene. So far as the mammals are concerned, this is chiefly indicated by the plains fauna. Owing to the generally higher temperature, the air was probably moister than at present, but the moisture may have carried farther, to be precipitated on the mountains. Thus the conditions on the plains and towards the sea may have resembled those of Southern and Lower California to-day, with a comparatively damp atmosphere but little or no preciptation during a considerable part of the year. The desert fauna and flora of the southwest is a highly specialized one, which has certainly not come into existence since the Miocene, at least as regards its fundamental types; so it becomes necessary to postulate a desert region during Miocene times, and no doubt much earlier. Whether we shall ever know much about the Tertiary deserts from fossil remains is perhaps questionable, though we certainly have evidence of a semi-desert fauna, as is illustrated by the large tortoises of the Upper Miocene. The Florissant beds afford us a wonderful insight into the mountain life of the Miocene, and must have a continually increasing significance in relation to the evolution of the fauna and flora of this continent. Most unfortunately, they have as yet yielded no recognizable mammalian remains, but I am convinced that these will eventually be found. The beds are far from being exhausted, and comparatively little digging has been done at the place where fragments of a mammal were obtained—a locality which I shall be glad to describe in detail to any one who cares to go and try his luck. In the meanwhile, large collections both of plants and of insects, already obtained, remain to be investigated and reported upon, but for various reasons the work proceeds slowly.

A SUGGESTION REGARDING HEAVY AND LIGHT SEED GRAIN[1]

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A CONSIDERABLE amount of work has been done by investigators of cereals, regarding the comparative value of heavy and light grains used as seed. The major portion of the experiments have been conducted with wheat, oats and barley. The problem appeared simple at the beginning, but has developed many complications.

In many cases bulk grain has been graded into various classes without determining the relative number of grains per measured quantity. Thus the experiments have been vitiated by the failure to consider the different rates of seeding, as regards the number of grains per area, which would naturally ensue. Even if allowance for seeding were made, and the number of grains per area determined as accurately as possible, it would be an excellent thing to conduct also a rate of sowing test. Such a test might throw light upon results induced by climatic conditions.

Some of the workers have made no distinction between shriveled grains and small plump grains. To eliminate the factor of shriveled grains would be virtually doing away with fanning mill methods of grading, which would seem to be necessary if we are to simplify the problem and to obviate the conflicting factors. Zavitz, of Ontario, has worked with small, hand-picked samples of grain and has evidently succeeded in overcoming the difficulties mentioned. His results, extending over a series of years, are remarkably consistent and worthy of careful study.

Despite some of the errors one can not fail to be impressed, as the literature is studied with the preponder-

[1] Contribution No. III, Laboratory Experimental Plant-breeding, Cornell University.

ance of evidence in favor of the large seed. The errors are as apt to tell against the heavy seed as against the light seed. In fact, where error has been most carefully eliminated, as in the experiment of Zavitz, the large seed gives the most striking positive results.

The result, empirically derived, while of great practical importance, does not throw much light on transmission. The majority of the experimenters have paid no attention to the *plants* from which the large or small grains have come. Bolley selected large and small grains from the same heads of wheat and found that the large grains generally produced the largest yields. Lyon has stated that both large and small grains in a lot of wheat must represent both large and small spikes, and if only large grains are sown one is not necessarily selecting from the best plants.

If, according to Johannsen,[2] "In a population containing only one single type, the selection of fluctuations has no action at all," then it would make no difference, as far as transmission is concerned, if all sorts of plants were represented in the seed, so long as we are dealing with a pure line. Most American breeders, however, would prefer to select for seed the best plants from the field each year, even if working with a pure strain. This practice is doubtless based on opinion at the present time rather than on well-grounded experimental knowledge. We ought to be willing to acknowledge our ignorance of the possibility of changing the type by selecting fluctuations of close pollinated cereals. Until more and accurate data can be secured a neutral position is much the better.

Correlation Data of Oats

The writer, in securing some statistical data on oats preparatory to breeding, noticed that the data were interesting in connection with the question of light and heavy seed. Measurements were taken on 1,000 oat culms grown at Dickinson, North Dakota, under field conditions. In nearly all cases, each head-bearing culm measured rep-

[2] Rpt. Third Int. Conf. on Genetics, London, 1906.

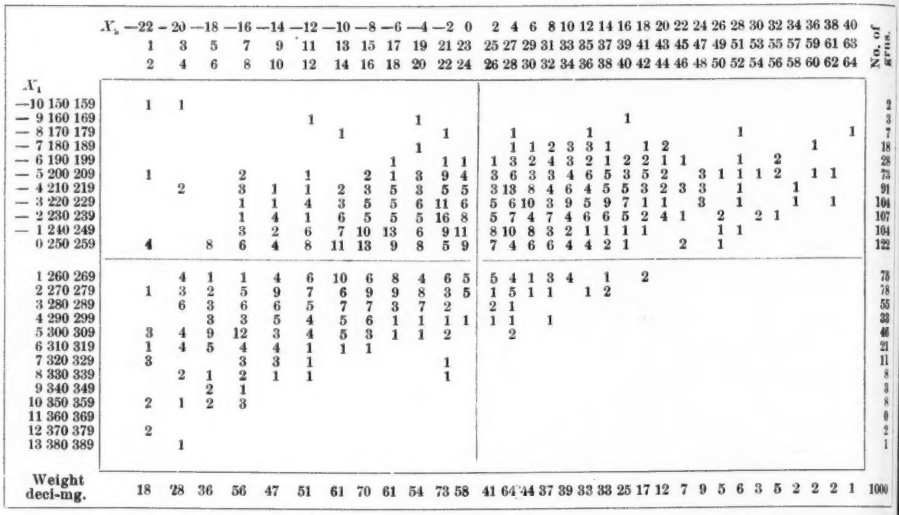

FIG. 1. Correlation in oats.[3] Average weight of grains subject, number of grains per head relative. Coefficient of correlation, -0.595 ± 0.013.

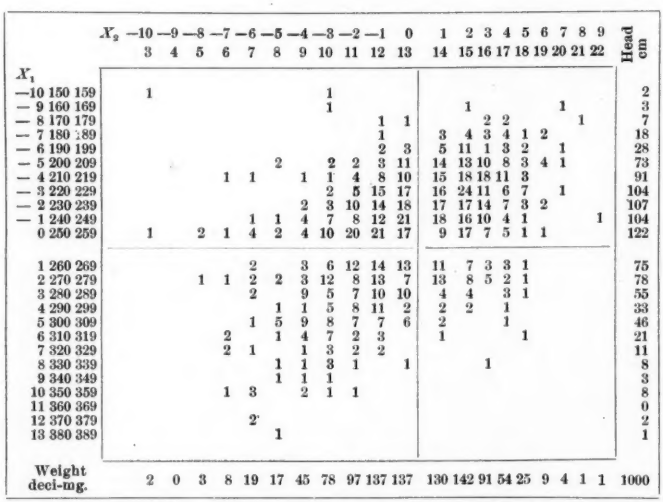

FIG. 2. Correlation in oats. Average weight of grains subject, length of head relative. Coefficient of correlation, -0.511 ± 0.015.

[3] The weights of the grains in the first five figures are expressed in decimilligrams. The lengths are expressed in centimeters. In Fig. 6 the weight is expressed in milligrams and the volume in cubic millimeters.

resented an entire plant. The variety is well defined morphologically, but evidently contains various races or biotypes.

Among other data secured was the height of culm, the length of head, the number of grains per head and the average weight of kernel. The various measurements were correlated and the results prove very interesting.

Fig. 1 shows the correlation existing between the average weight of kernel as subject and the number of grains per head as relative. A strong negative correlation is noticed, amounting to very nearly 60 per cent. In other words, the greater the number of grains per head, or, in reality, the larger the head as regards grain, the less the average weight per kernel.

The mean of the number of grains per head, of the population studied, is 22.098 and the mean weight per kernel is 24.913 mg.

The regression coefficient of the number of grains relative to the average weight of grain is — 1.98. In other words, if we should select grains for planting that weigh, for instance, 30 mg. and above, they would on the whole be selected from heads containing only about 12 or 13 grains, which represent heads considerably below the mean. There would doubtless be an occasional grain from heads above the mean, but such grains would be uncommon and the increasingly larger heads would be more and more sparsely represented in the grain selected for planting.

Fig. 2 shows the correlation existing between the average weight of kernel as subject and the length of head as relative. As the number of grains is quite dependent upon the length of head we should expect to find a correlation existing between the two, somewhat similar, as is shown in Fig. 1. The actual correlation is negative and amounts to 51 per cent. The mean length of the head is 13.583 cm.

The regression coefficient of the length of the head relative to the average weight of grains is — 0.379. That is, if we should select grains for planting that weigh, for instance, 30 mg. and above, they would in general be

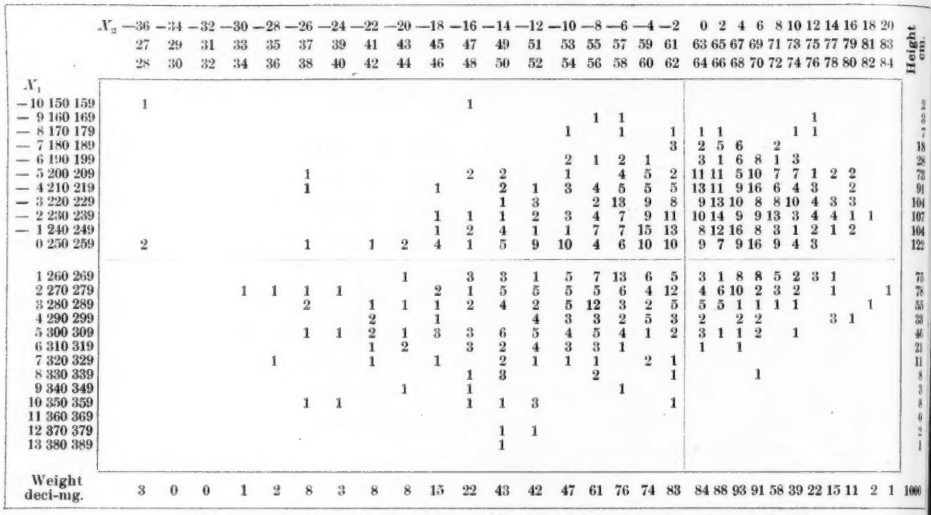

FIG. 3. Correlation in oats. Average weight of grains subject, length of culm relative. Coefficient of correlation, -0.404 ± 0.017.

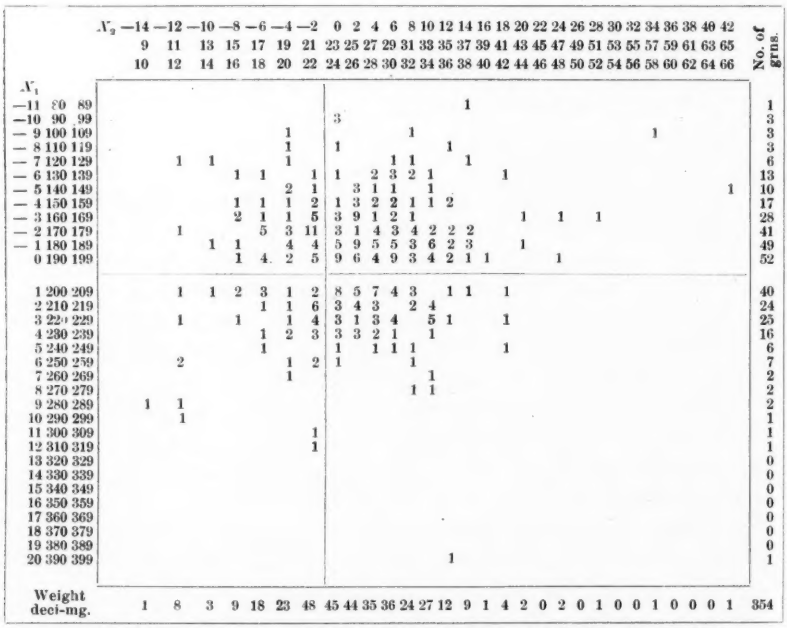

FIG. 4. Correlation in winter wheat. Average weight of grains subject, average number of grains per head relative. Coefficient of correlation, -0.115 ± 0.031.

selected from heads in the neighborhood of 11.5 cm. long. We should have to select the shorter heads in order to secure the larger grains.

Fig. 3 shows the correlation existing between the average weight of kernel as subject, and the total height of culm, including the head, as relative. The correlation is still negative and amounts to 40 per cent. The mean length of the culm is 61.74 cm.

The regression coefficient of the length of the culm relative to the average weight of grain is — 0.987. As in the last example, the selection of grains weighing 30 mg. and above would imply that they had come from culms about 56 cm. long, or about 5 cm. below the mean.

As a summary, plants with shorter culms, shorter heads, and with a smaller number of grains, bear on the whole grains of a greater weight. The opposite of course is equally true.

If the data had been taken of a pure strain of oats, of the variety studied—of a number of plants that had come within a few generations from a single mother plant—then the correlations might have varied slightly from those given. If data were accessible of another variety, then we might suspect even greater deviation from the figures given. Variation in the same variety from year to year may be expected. However, there is nothing to lead us to believe, from an *a priori* standpoint, that the data given would be essentially changed.

If data were taken on oat plants grown in hills, then we might get less decided negative correlations than those given where the plants were grown under field conditions. The variability of the number of grains, the height of plant and the length of head might be less, while the variability of the average weight of grain might not be much different.

The following table shows the coefficients of variability expressed in per cent. of the various factors that have been discussed.

The factor of the number of grains is evidently the much more variable one and perhaps under hill condi-

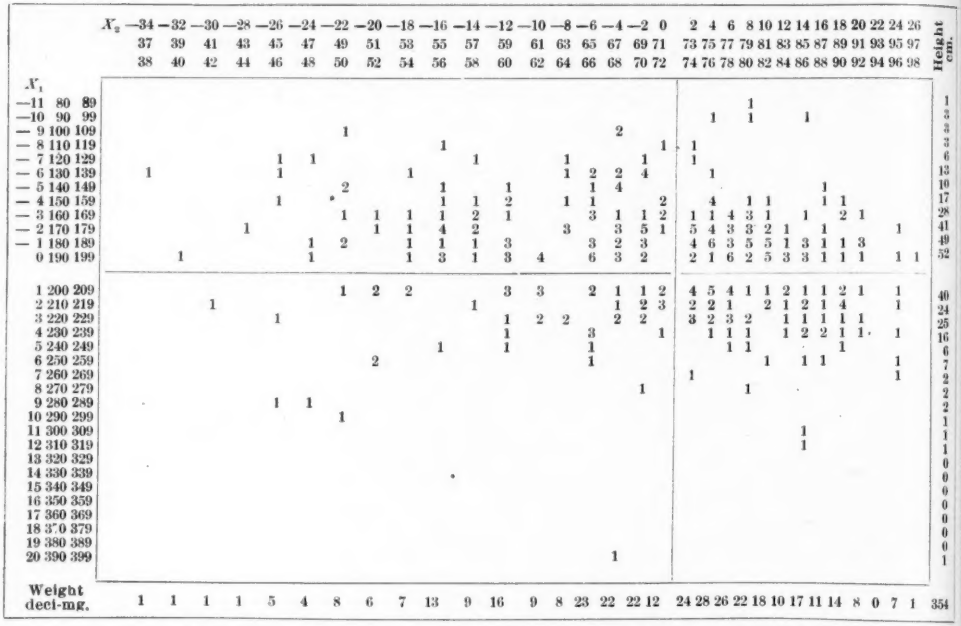

FIG. 5. Correlation in winter wheat. Average weight of grains subject, average length of culm relative. Coefficient of correlation, 0.16 ± 0.034.

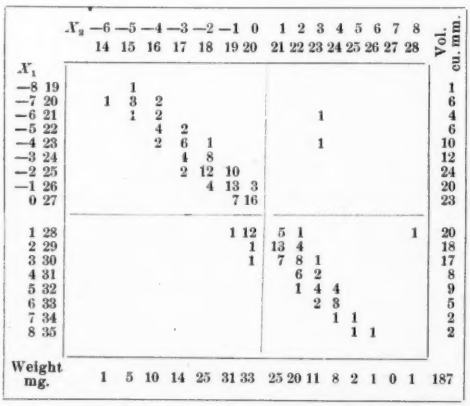

FIG. 6. Correlation in winter wheat. Average weight of grains subject, average volume of grains relative. Coefficient of correlation, 0.896 ± 0.009.

tions it would be somewhat reduced, though this is only problematical.

Factor.	Coefficient of Variability.
Number of grains	54.5 ± 2.33
Average weight of grains	14.5 ± 0.48
Length of head	19.7 ± 0.68
Length of culm	14.2 ± 0.47

Since the above was written it has been found that the small oat heads bear a somewhat larger percentage of single grains than the large heads. If this factor be considered, the negative correlations would be somewhat decreased but probably not materially.

Correlation Data of Wheat

In looking over the literature some unreduced winter wheat data were found in Bulletin 78 of the Bureau of Plant Industry by Dr. T. L. Lyon. A portion of this data was thrown on to correlation tables and is given herewith.

Fig. 4 shows the correlation existing between the average weight of kernel as subject and the average number of grains per head as relative. Both the weight and number are averages for the entire plant. The figures are thus not quite comparable to those given for the oat plants, but are doubtless nearly so. Data for only 354 individual plants are given, but this number of plants represents a considerably larger number of culms. The correlation is negative and is a little over 11 per cent. The regression of the average number of grains relative to the average weight of grains is much diminished and a selection of seed of either very high or of very low weight would not indicate that the seed was from plants located any appreciable distance from the mean, as far as average number of grains is concerned.

Fig. 5 shows the correlation existing in winter wheat between the average weight of kernel as subject and the average height of culm as relative. As in the previous case, data for only 354 individuals are given. Instead of a negative correlation, as in all previous cases, we have

here a positive correlation, amounting to 16 per cent. This is a weak correlation. The regression of the average height of culms is very slight. Selection of any particular weight of seed would not imply that any particular heights of plants were involved.

It is interesting to note that the correlations given of winter wheat hold about the same relations to each other as do the corresponding correlations of the oats.

RELATION OF SIZE TO VOLUME OF GRAIN

But little accurate data on this point are available. We should expect to find a close correlation. The data given in Fig. 6 are taken from Bulletin No. 78 mentioned previously. It is seen that there is an almost perfect correlation existing between the average weight of kernel and the average volume per kernel. The three outstanding individuals suggest errors rather than extreme variations.

SUMMARY

If oat populations in general show constants similar to those given, then the experimenter selecting the large grains is not selecting from what is commonly considered the best plants, and *vice versa*. If the plants from large grains produce a better yield, then they must do so by virtue of the increased vigor of the embryo and the increased amount of food supply. If we consider that the size and yield of the mother plant have an influence upon the size and yield of the daughter plants, then we must consider that this influence is decidedly less than the influence exerted by the size of the seed. If the size and yield of the mother plant have no effect upon the offspring, then we might expect the yields from different weights of seed to be somewhat in proportion to the weights of seed.

Despite all that has been written on the foregoing points we have very little accurate knowledge pertaining thereto, especially relative to the influence of selection upon the close pollinated cereals.

NOTES AND LITERATURE

MAMMALOGY

Nelson's Monograph of the North American Leporidæ.—Mammalogists owe a debt of gratitude to Mr. E. W. Nelson for his recent monographic revision of the hares and rabbits of North America,[1] the first revision of the group as a whole since the publication of Allen's monograph of this group in 1877. Mr. Nelson, in addition to abundant material, has brought to his task an intimate knowledge of these animals in life, and of the environments to which the different groups of species are subjected, through his many years' experience as an explorer and collector, covering a wide area, embracing Arctic Alaska, the arid southwestern United States, Lower California, and the whole of Mexico, including the tropical coast lands as well as the plateau region. The monograph is based on the careful study of nearly 6,000 specimens, all of the material contained in the principal museums of America having been examined. The number of species and subspecies recognized is 97, of which 93 are contained in the collections of the United States National Museum. This is an increase of nearly 80 over the number known in 1877.

The introduction (pp. 9–61) deals with the economic relations of the American rabbits to agriculture; the use of the names rabbit and hare; the condition of the young at birth; the distribution of the genera and species; their habits and diseases; their color patterns, molts and seasonal changes of color; sexual, individual and geographic variation; their classification, and keys to the species and subspecies.

Points of general interest are the destructiveness of these animals to vegetation, through injury to young trees, both in orchards and newly planted forests; and their food value, which, as is well known, is considerable, millions of rabbits being sold in our markets each winter.

The names hare and rabbit were originally used in a specific

[1] "The Rabbits of North America," by E. W. Nelson, chief field naturalist, Biological Survey. Prepared under the direction of Dr. C. Hart Merriam, Chief of Bureau of Biological Survey. North American Fauna, No. 29, August 31, 1909. 8vo, pp. 1–314, pl. i–xiii, and 19 text figures.

sense to designate the two long-known European species; later their use became greatly broadened and their application more or less interchangeable, with different restrictions by different authorities and in different countries. Mr. Nelson would confine the use of the term hare, so far as American species are concerned, to the restricted genus Lepus (including the varying and Arctic hares and the jack rabbits), and employ the term rabbit for the "cotton-tails" or smaller brush rabbits and swamp rabbits (genus Sylvilagus and allied forms). The hares are, generally speaking, larger than the rabbits, live mostly in "forms," and bring forth young with open eyes and well-clothed with hair; many of the rabbits are known to bring forth their young naked and blind; while some of them burrow, others live in forms, like the true hares.

Formerly all the species of Leporidæ were referred to the single genus Lepus, but later, mainly within the last decade, several genera have been recognized by the leading authorities on the group, together with a number of subgenera. Mr. Nelson arranges the North American species in four genera—Lepus, Sylvilagus, Brachylagus and Romerolagus. The last two are monotypic with very restricted ranges; the rest of the species are assigned to Lepus (with two subgenera, Lepus = Arctic and varying hares, and Macrotolagus = "jack rabbits") and Sylvilagus (also with two subgenera, Sylvilagus = "cotton-tails" or brush rabbits) and Tapeti (swamp rabbits. The latter includes most of the species of Central and South America).

The hares of the subgenus Lepus (the Arctic and varying hares) have a double molt, being brown in summer and white in winter, while the other species are believed to molt, for the most part at least, only once (in fall), and the only seasonal change of color is due to the fading and abrasion of the long-worn coat. Formerly it was supposed that the white winter coat of all the northern hares was due to a change of color in the hair itself of the summer coat. On this point Mr. Nelson says:

> The change in color from the white winter pelage of northern species to the dark summer coat, or *vice versa,* is accomplished so gradually that at certain stages it appears like a change in the color of the hairs instead of a molt, as was definitely proved by Doctor Allen in his paper on the changes of pelage of the varying hare.[2]

This supposed change of color in the hairs, he further says,

[2] *Bull. Am. Mus. Nat. Hist.,* VI, pp. 107–128, May 7, 1894.

"may be readily disproved by a careful examination of a few molting specimens." It is also now well known that the white winter coat of the ermines and weasels, and of such species of lemmings as turn white in winter, is due to molt and not to a blanching of the hairs of the summer coat. In other words, seasonal change of color in mammals, as well as in birds, is due entirely to molt. In the case of the hares and weasels, the change to white in winter is only partial at the southern border of the ranges of species that further north become wholly white in winter, while the most northern forms of the Arctic hare group remain practically white in summer, as in northern Greenland and northern Ellesmere Land. The time of molt also varies with the character of the season. As has long been known, an early spring or fall brings on the molt a month or more earlier than a later one, and hence a change of color in such species as have a white winter livery is correspondingly later.

Mr. Nelson confirms the statements of previous writers that the pelage in mammals is in other ways subject to modification by the environment, as through variation in its length and density in accordance with the severity of the climate. In discussing the effect of environment, he also confirms the experience of other mammalogists, and of ornithologists and herpetologists as well, that "like climatic conditions often produce the same or closely similar colors in dissimilar species," and also parallel modifications in other features, including cranial details of structure.

> These fluctuations are somewhat wavelike in character and rise to central points of extreme development and then sink away to intermediate borders beyond which new waves arise. When the waves of differentiation are pronounced they mark recognizable geographic races. . . . In the case of wide-ranging subspecies such fluctuations are frequent, especially where the areas occupied are diversified by mountains. These fluctuations, which are sometimes extremely local, mark, of course, potential subspecies. Some are fairly well characterized and eventually may be named, while others are too slight to be formally recognized by name, but well serve to illustrate the plastic condition of the species. The transition from one subspecies to another takes place abruptly or gradually in exact accord with the changes of environment which produce them. . . .

As is well known, many mammals are subject to periodic destruction by disease. This is especially marked among rodents,

such as voles, ground-squirrels and rabbits, and their reduction or increase in numbers, as the case may be, powerfully affects the welfare of such species of mammals and birds as prey upon them. In the case of rabbits, destruction by epidemics is periodical, occurring apparently about once in seven years, although exact data are wanting as to the regularity or frequency of these epidemics, or their exact nature. They are at times so severe that only a few individuals are left to perpetuate the species. They are also followed, there is some reason to believe, by an increased birthrate by which the stock is rapidly replenished. This periodic destruction is considered by Mr. Nelson in relation to the apparent opportunity thus afforded for the origination, through isolation, of many strongly characterized forms, but he fails to find evidence that this is an evolutionary force of much importance. The *Lepus americanus* group, occupying the vast wooded area from Nova Scotia to western Alaska, which has been subjected to numberless recurring periods of extreme abundance and extreme scarcity, presents only a few, and not strongly, differentiated subspecies, owing, it is believed, to the leveling influence of similarity of climate.

In illustration, however, of the effects of complete isolation under similar climatic conditions, the black jack rabbit of the island of Espiritu Santo is cited. This small island lies off La Paz Bay, Lower California, only four miles from the mainland, from which it is separated by a channel having in its shallower parts only four to five fathoms of water. The island was doubtless formerly a part of the mainland, and has still the same character of vegetation and climate. The adjacent mainland is occupied by a pale form of the *Lepus californicus* group, the island by a form essentially the same in size and cranial characters, but so dark in color as to be commonly referred to as the "black" jack rabbit. The intensification of color, making it "extraordinarily conspicuous," has not been "protective," nor yet has it proved a detriment, presumably from the fact that no predatory mammal or large bird of prey shares its habitat.

Coming now to the systematic portion of the monograph, it may be noted that the genera and subgenera here recognized are very satisfactorily characterized, and the keys to the species and subspecies are carefully elaborated, occupying ten pages for the 97 forms recognized. These, in the systematic part of the monograph, are treated very fully in respect to their distinctive char-

acters, ranges and relationships. There is, however, very little on the historical side of the subject beyond a briefly annotated bibliography of sixty-six titles (pp. 282–287), prefaced by a page and a half of historical résumé. The citations under the species relate almost wholly to synonyms, which in this group of American mammals are fortunately exceptionally few. There is little to indicate the point of view of previous writers, or their manner of treatment as regards forms recognized and their allocation. The correlation, from the author's standpoint, of work previously done is an essential feature of a monographic treatise; and this can be fairly shown in tables of reference,[3] with such slight additional comment as may seem necessary. This defect in the present case is doubtless a feature of environment, due to limitations already referred to in another connection.[4] Yet it seems strange to find no reference under the genus Romerolagus to the discussion of the structure and affinities of this interesting type by previous authors, as Lyon, Major and Herrara, nor to the alleged earlier competitive name for the species, namely *Lepus diazi* Ferrari Perez (1893).

As already intimated, the systematic treatment is in general excellent. The species is first considered as a whole; its subspecific components are passed in review, their ranges shown graphically on a map, and a table gives the average measurements, external and cranial, of five specimens of each form, the same external measurements being repeated later in their proper connection in the text. This number, however, is too few to be satisfactory, and extremes of variation are not indicated. Under the subspecies the geographic range is first indicated, followed by a paragraph of "general characters," and very full descriptions of the coloration, seasonal variations, cranial distinctions, and such "remarks" as circumstances may require. In view of the material studied by the author, and his standing as an investigator, criticism of details would be out of place unless based on equal opportunities. Mr. Nelson, however, has given a decidedly new aspect to the nomenclature of the group, through the revival of certain previously unidentified names, the merging of the *texianus* group of former authors with the *californicus* group, of the *arizonæ* group with the *audu-*

[3] Note, for example, the synonymies in Ridgway's "Birds of North and Middle America."

[4] AMERICAN NATURALIST, Vol. XLIII, October, 1909, p. 639.

boni group, the reduction to subspecies of numerous forms previously recognized as species, and the raising to specific rank of forms formerly treated as subspecies.

The only new form appears to be a subspecies *littoralis* of *Lepus aquaticus* Bachman, through the assignment of a type locality for *aquaticus*. As Mr. Nelson says, there "was no definite type," and the species was described "from specimens obtained in western Alabama by Dr. J. M. Lee. . . . No definite type locality is mentioned, but the context appears to indicate that these specimens came from western Alabama, which may be considered the type region." He further states that "the types do not appear to have been preserved," and were thus unavailable as an aid in settling the type locality. In the original account of this species Dr. Bachman said that he did not know of its existence "to the east or north of the State of Alabama," but that "it is numerous in all the swamps of the western parts of that state, is still more abundant in the State of Mississippi and the *lower parts*[5] of Louisiana, and is frequently brought by the Indians to the market of New Orleans." If Mr. Nelson had been the first to split the *Lepus aquaticus* group into a Gulf coast form and an interior form his course would be justifiable, but this division was made long before, when the *Lepus aquaticus attwateri* was separated on the basis of comparison of specimens from the vicinity of San Antonio, Texas, with a series from the vicinity of New Orleans. He recognizes only the same two forms, so that his *littoralis* is properly a synonym of *Lepus aquaticus aquaticus*, with the name of the interior form still *Lepus aquaticus attwateri*. Were it conclusively known that the type locality of *aquaticus* was within the range of the interior form, he would be fully justified in his present ruling, but in view of the fact that it is at best conjectural, and that the same division of the species he now makes had been made before, thus in effect restricting the name *aquaticus* to the Gulf coast form, his action in the case seems at least open to reasonable objection.

The illustrations comprise twelve excellent plates (from photographs) of skulls of the different leading types of North American hares and rabbits, a plate (from a wash drawing) of "directive coloration in *Lepus callotis*," and nineteen text figures, sixteen of which are distribution maps, and three illustrate osteological characters in the genera Lepus and Sylvilagus.

[5] Not italicized in the original.

The "directive coloration" plate shows two specimens of a Mexican species of jack rabbit, which has white sides and a dark buffy mantle covering the back. One figure shows the mantle in its usual position, the other with the mantle "shifted to the opposite side and the whitish area of the side drawn up nearly or quite to the dorsal line," the animal being then in the act of "signalling." This extraordinary feat is described at length on page 115, where it is said that "By means of muscles the skin of either side can be drawn over the back at will." Mr. Nelson further states that on one occasion one of these rabbits observed by him kept the "white area in the same position until it had traveled 50 or 60 yards, when the colors slowly resumed their normal positions."

Despite the slight criticisms we have felt called upon to make, Mr. Nelson's "The Rabbits of North America" marks an era in the history of the group, and is so comprehensive and so well done that it must long remain the basis for future work, to be corrected doubtless in many minor details as new material is received, but nevertheless a boon to all workers in North American mammalogy.

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NEUROLOGY

Edinger's "Vorlesungen über den Bau der nervösen Centralorgane" made its first appearance as a small volume in 1885. Its directness and lucidity gained for it at once a deserved popularity and a growing demand justified the numerous editions under which it subsequently appeared. In its latest form, the seventh edition, the work consists of two volumes, either of which is about twice the size of the original edition. This considerable expansion has taken the work away from the circle of readers, mostly medical students and physicians, for whom the earlier editions were intended. It is therefore natural that an effort should be made to return to the earlier form and this effort has found its realization in the present "Introduction."[1] This volume, which contains a little less than two hundred pages, is a

[1] Edinger, L., "Einführung in die Lehre vom Bau und den Verrichtungen des Nervenssystems." Leipzig, F. C. W. Vogel, 190 pp., 161 figures, 1 plate, 1909.

summary of the larger work, but with the emphasis laid on the human central nervous organs. The presentation has the great advantage of beginning with the consideration of the spinal cord, the more primitive part of the central nervous system, and then proceeding to the more specialized part, the brain, instead of dealing with these subjects in the reverse order as in the early editions of the "Lectures." The condensation has been most admirably done, and, as a work that is intended to state briefly those matters that are best established for the structure of the central nervous organs in man, it is a masterpiece. The regrets that one may have about the volume are chiefly because of omissions, but condensation implies omissions and it is hard to imagine under the circumstances a better selection of materials. In one respect the general presentation might perhaps have been improved. It is strange that Dr. Edinger, who accepts the neurone theory so completely, should have abandoned this method of presentation in dealing with the brain, though he adopts it in his account of the cord. Possibly, however, the greater uncertainty of resolving the brain from the standpoint of the neurone as compared with the cord, is a justification for this difference of treatment. In illustration and typography the volume is on as high a level as in subject matter.

G. H. PARKER.